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Atilax paludinosus. By C. M. Baker

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Atilax Cuvier, 1826

Atilax Cuvier, 1826:2. Based on the "Vansire" of F. Cuvier [=Herpestes paludinosus Cuvier, 1829 (see Allen, 1924:171)]. Athylax De Blainville, 1837:272. Unjustifiable emendation of Atilax Cuvier, 1826.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Feliformia, Family Herpestidae, Subfamily Herpestinae. The genus Atilax is monotypic (Meester et al., 1986).

Atilax paludinosus (Cuvier, 1829)

Marsh Mongoose

H[erpestes]. paludinosus Cuvier, 1829:158. Type locality "marais du Cap [=Cape of Good Hope]," South Africa.

Mangusta urinatrix Smith, 1829:437. Type locality "South Afri-

ca.

Herpestes atilax Wagner, 1841:305. Type locality "Sudafrica." Atilax vansire Cuvier in Geoffroy and Cuvier, 1842:3. Names the 'Vansire'; see under Atilax above.

Herpestes pluto Temminck, 1853:95. Type locality "Dabocrom," Gold Coast [=Ghana].

Athylax paludosus Gray, 1865:557. Name emendation.
Athylax robustus Gray, 1865:558. Type locality "White Nile," Sudan.

Atilax macrodon Allen, 1924:205. Type locality "Niapu, Belgian Congo" [=Zaire].

CONTEXT AND CONTENT. Context as for the genus. The species Atilax paludinosus is divided into 10 subspecies. A. p. guineensis may be regarded as a synonym of A. p. pluto (Coetzee,

- A. p. macrodon Allen, 1924:205, see above.
- A. p. mitis (Thomas, 1903:309). Type locality "Zegi, Lake Tsana, 4000 feet," Ethiopia.
- A. p. mordax (Thomas, 1912:588). Type locality "Rombashi River in German E. Africa, N.W. of north end of Lake Nyasa,' Tanzania.
- A. p. paludinosus (Cuvier, 1829:158), see above (includes urinatrix, atilax, vansire, and paludosus).
- A. p. pluto (Temminck, 1853:95), see above.
- A. p. robustus Gray, 1865:558, see above.
- A. p. rubellus (Thomas and Wroughton, 1908:166). Type locality "Tambarara, Gorongoza Dist., Portuguese East Africa" [=Mozambique].
- A. p. rubescens (Hollister, 1912:1). Type locality "Mount Kilimanjaro, East Africa, at 4000 feet," Tanzania.

 A. p. spadiceus Cabrera, 1921:262. Type locality "Cabe San Juan
- (Guinea española) [=Equatorial Guinea]."
- A. p. transvaalensis Roberts, 1933:266. Type locality "Mokeetsi, N. Transvaal," South Africa.

DIAGNOSIS. Skull is broad (Fig. 1) with zygomatic breadth averaging 58% of condylobasal length (Rosevear, 1974) and condylo-incisive length >100 mm in adults (Coetzee, 1977). Supraoccipital crest is flange-like. In Ichneumia it rises up approximately 4-5 mm above the surface of the braincase, while in Herpestes ichneumon it rises approximately 7 mm from the skull. Sagittal crest well developed in adult marsh mongooses (up to 4 mm in height) and meets supraoccipital crest to form a "T." Saggittal crest in Ichneumia and Herpestes ichneumon is distinct but not as well developed as in Atilax. Braincase pear-shaped with marked postorbital constriction, but in Ichneumia and Herpestes ichneumon is ovoid and more elongate. Postorbital processes elongated and may meet jugal processes to form an orbital ring in older animals. Eye sockets small relative to skull length, with diameter at widest point

20% of condylobasal length. Frontal region broad and slightly inflated. Rostrum short and broad in Atilax and Ichneumia. In Herpestes ichneumon rostrum short and narrow. Zygomatic width >50% of total skull length. Bulla of Atilax with inflated posterior chamber. Lower jaw broad and heavy; coronoid process wide and high (Rosevear, 1974; Skinner and Smithers, 1990; Smithers, 1983).

Incisors set in a straight transverse row. Upper and lower outer incisors longer than others. In Ichneumia upper incisors have a shelf



Fig. 1. Dorsal, ventral and lateral views of cranium, and lateral view of mandible of Atilax paludinosus, male (Durban Museum 135) from Richmond, South Africa. Greatest length of skull

MAMMALIAN SPECIES 408

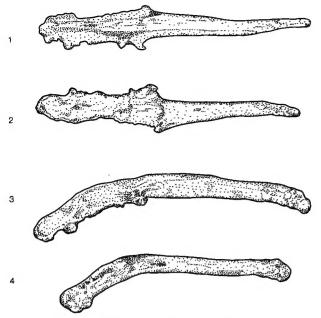


Fig. 2. Dorsal (1), ventral (2), and lateral (3) view of baculum from adult and lateral (4) view of baculum from juvenile *Atilax paludinosus robustus* (redrawn from Didier, 1948).

on the inner side caused by tooth wear. Canines of marsh mongoose heavy and more curved in lower jaw. Upper canines with blade-like processes on front and back. The fourth upper premolar tends to wear flat and M1 has blunt rounded cusps (Skinner and Smithers, 1990; Smithers, 1983). Adult baculum is convex (Fig. 2), measuring 18 mm in length, and broadens ventrally (Didier, 1948).

Geographic variation in color occurs (Coetzee, 1977) and may be used to distinguish among subspecies (Smithers, 1983). Externally, Atilax paludinosus may be distinguishable from the other two large herpestines, Ichneumia albicauda and Herpestes ichneumon, because it lacks the white tail of the former and the broad black tail-tip of the latter (Smithers, 1983).

GENERAL CHARACTERS. Mean mass of males and females from Zimbabwe (n=12 for each sex) is 3,400 g (Smithers, 1983). Mass approximately 2,000–5,450 g in southern Africa (Rowe-Rowe, 1978; Smithers, 1983; Stuart, 1981). In Botswana, Smithers (1971) recorded mass as 4,031–5,113 g. Slight sexual dimorphism occurs; females being smaller than males. Average mass of females is 2,562 g (n=9) and males 2,956 g (n=18; Stuart, 1981). Body shape is long, legs are short and the tail measures approximately 66% of length of head and body (Fig. 3). Mean body measurements (in mm) for southern African males and females, respectively, are as follows: length of head and body, 513.8 (n=38), 487.2 (n=32); length of tail, 341.1 (n=40), 321.8 (n=31); length of hind



Fig. 3. Female Atilax paludinosus from Hilton, South Africa.

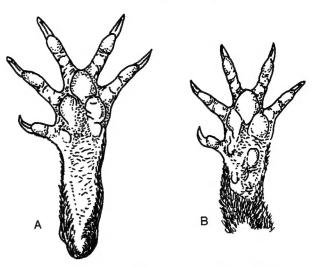


Fig. 4. Left forefoot (A) and hind foot (B) of Atilax paludinosus (redrawn from Pocock, 1916).

foot, 105.9 (n = 39), 100.9 (n = 31); length of ear, 34.6 (n =41), 32.5 (n = 31; Maddock, 1988; Rautenbach, 1982; Rowe-Rowe, 1978; Smithers and Wilson, 1979; Stuart, 1981). In West Africa mean body measurements (in mm, range in parentheses) for males and females together (n = 20) are as follows: length of head and body, 501 (442-553); length of tail, 322 (250-355); length of hind foot, 96 (84-102); length of ear, 33 (28-40; Rosevear, 1974). Overall shaggy appearance is conferred by long, coarse guard hairs, which are often annulated, imparting a grizzled appearance. Underfur is soft and woolly. Color varies from a rich reddish-brown through black. Eyes are small with horizontal pupils. Rhinarium is broad and pink and black or wholly black; a slit down the front divides the hair on the upper lip. External nares are dorsolaterally situated. Ears are broad and round and basally obscured by hair. Feet have five toes and well-defined digits that lack webbing (Fig. 4). Plantar surfaces are smooth and naked (Pocock, 1916; Smithers, 1983). Claws are curved and short (Smithers, 1983). Anal glands are located within an anal pouch (Fig. 5) and produce a volatile musky secretion. Cheek glands produce less odoriferous secretions (Baker, 1988a).

DISTRIBUTION. The marsh mongoose is found throughout most of Africa south of the Sahara (Fig. 6). In southern Africa it occurs in southern and eastern Cape Province; Natal; eastern Orange Free State; Transvaal; eastern and central Zimbabwe; extreme northern western Botswana; and extreme northeastern and northern Namibia (Meester et al., 1986). In western Africa the species is known from Senegal, Guinea Bissau, Sierra Leone, Nigeria, Benin, Ghana, Liberia, Cameroon, Equatorial Guinea, and Gabon (Dekeyser, 1955; Rosevear, 1974). In central and northeastern Africa it is found in southwestern Ethiopia, southern Sudan, Zaire, Congo Republic, Uganda, and Angola and in eastern Africa in southern and western Kenya, Tanzania, Malawi, and Mozambique (Skinner and Smithers, 1990).

FOSSIL RECORD. A mid-Pleistocene fossil, Herpestes mesotes, from the Kromdraai deposits in the Transvaal, South Africa, is believed to be the direct ancestor of Atilax paludinosus (Ewer, 1956). Tooth pattern and palate shape of Herpestes mesotes indicate a close relationship with H. ichneumon. A tooth and mandibular fragment of Atilax from Olduvai Site suggest close affinity with Herpestes (Petter, 1973). This fossil dates from the Pleistocene.

FORM AND FUNCTION. Upper parts of the marsh mongoose are uniformly colored, varying from deep russet to black. Guard hairs are longest in the flank region and at the base of the tail. In West Africa hair length ranges from 32 to 44 mm (Rosevear, 1974) and from 45 to 50 mm in Zimbabwe (Smithers, 1983). Annulations on the hairs may vary in width and may be either white, off-white, reddish brown, or russet. Their presence confers a grizzled appearance (Smithers, 1983). Underfur varies in length from 15 mm to 25 mm (Rosevear, 1974; Smithers, 1983). Color varies from dark greyish-brown to reddish brown (Smithers, 1983). Hair is short

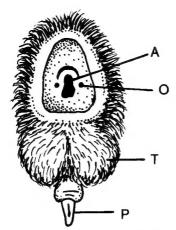


Fig. 5. Anal pouch of male Atilax pulled open to display openings of anal sacs (O) on either side of the anus (A); (P) penis; (T) testis (redrawn from Pocock, 1916).

and fawn-colored around the mouth, limbs are uniformly dark, either black or deep brown (Baker, 1988a).

The tongue of the marsh mongoose bears one pair of circumvallate papillae which are the main gustatory organs (Sonntag, 1923). Papillae clavatae, lateral organs, and lateral glands are absent. There is an anterior spinous patch of conical papillae with well-developed points. Conical papillae on the base are small and the ventral surface of the tongue is plain, with a well-marked frenum (Sonntag, 1923).

Two pairs of mammae are present in specimens from Natal, South Africa (Baker, 1988b). Two pairs (one pair inguinal and the other abdominal) are recorded from specimens in Zambia (Ansell, 1960). Three pairs of abdominal mammae were found in Zimbabwe (Smithers, 1983). While more than one pair of mammae may exist, only one pair is functional (Kingdon, 1977).

The long digits are unwebbed and both hallux and pollex are long, unlike those of other herpestines (Pocock, 1916). The baculum is shorter in juveniles (15 mm) than in adults (18 mm; Fig. 2). The ventral surface is grooved posteriorly and when viewed dorsally curves to one side (Didier, 1948).

Dental formula is i 3/3, c 1/1, p 3-4/3-4, and m 2/2, total 36-40. Marked variation in the presence of the first premolar in both upper and lower jaws occurs. From 26 skulls from west Africa, the following variations in premolars were recorded: 3/3 (n = 9); 4/4 (n = 6); 4/3 (n = 5); 3/2 (n = 1); 2/2 (n = 1 juvenile). The remaining four specimens showed the following: 4/4-3; 4/3-2; 4/2-1; 3/3-2 (Rosevear, 1974).

The distal articular surface of the radius is not deeply set into the ulna and bears a process on the posterior margin that emphasizes the concave nature of the articular surface (Taylor, 1974). The ramus of the pubis is slender and the associated adductor musculature is reduced. In general the metatarsals are not closely adjoined, thus allowing space for interossei. The fifth metatarsal is wide mediolaterally and the lateral process is small. Length (in mm) of hindlimbs and forelimbs of a single male adult are as follows: pubis, 82; femur, 83.2; tibia, 103.9; scapula, 56; humerus, 83.3; ulna, 92.6; olecranon, 14.9; and radius, 74.8 (Taylor, 1974, 1976).

The neuroanatomy of the cortex suggests an elaboration of tactile sensitivity and motor control of the feet, thus allowing considerable manual dexterity (Radinsky, 1975). An encephalization quotient of 0.81 (Sheppey and Bernard, 1984) shows a positive correlation between body mass and feeding efficiency. A brain mass of 28.5 g suggests a relationship to type of breeding group and foraging strategy (Gittleman, 1986).

Paired anal glands are located within an anal sac and open to the exterior on either side of the anus (Fig. 5; Ewer, 1973; Pocock, 1916). Data on histology are lacking. Cheek glands are less well developed and are situated near the base of the genal vibrissae (Baker, 1988a).

A blood sample from a marsh mongoose exhibited three hemoglobin components with electrophoretic mobilities, relative to hemoglobin A of humans, ranging from 0.85 to 1.15. Electrophoretic patterns of hemoglobins in a variety of viverrids show no relationship with taxonomic groupings (Seal, 1969).

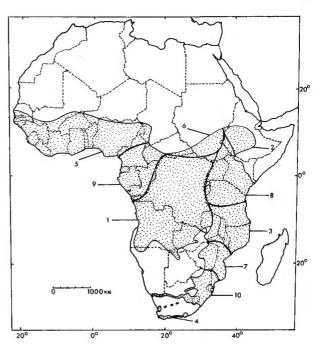


Fig. 6. Geographical distribution of Atilax paludinosus (from Smithers, 1983): 1, A. p. macrodon; 2, A. p. mitis; 3, A. p. mordax; 4, A. p. paludinosus; 5, A. p. pluto; 6, A. p. robustus; 7, A. p. rubellus; 8, A. p. rubescens; 9, A. p. spadiceus; 10, A. p. transvaalensis.

ONTOGENY AND REPRODUCTION. In East Africa a female was seen with a juvenile in June and in August well-developed fetuses were found (Kingdon, 1977; Loveridge, 1923). Breeding occurs in summer in southern Africa and the season extends from September through December (Ansell, 1960; Rowe-Rowe, 1978; Smithers, 1971). In captivity, litters are born as late as March and gestation varies from 69 to 80 days ($\bar{X} = 74.1$ days, n = 6). Litter size varies from 2 to 3 ($\bar{X} = 2.5$) and the sex ratio is not significantly different from 1:1 (Baker and Meester, 1986).

At birth, marsh mongooses are uniformly black and the hair is soft and wavy; pinnae are unfolded and the auditory meatus is closed; eyes are closed; toes are separated and the claws are soft; incisors 1 and 2 are present. Mean birth mass ranges from 78 to 122.7 g with $\bar{X}=108.5$ g (Baker and Meester, 1986; Frese, 1981). Individual postnatal growth rate is approximately 14.3 g/day (Oftedal and Gittleman, 1989).

The pelage becomes progressively grizzled from day 26. Eye opening ranges from day 9 to day 14 and onset of hearing occurs on approximately day 20. The earliest that weaning commences is day 30, but the young continue to suckle until approximately 8 weeks old. Order of tooth eruption in captive animals is i 3, c 1, p 3, p 2, and p 1. However, in one wild-caught male from Durban, South Africa, the order of premolar eruption was p 1, p 2, and p 3. The deciduous set is complete by approximately day 44 and the permanent set by approximately day 243. Male young are born with abdominal testes and time of descent varies from day 204 to 307. Adult mass is attained at approximately 27 weeks (Baker and Meester, 1986). In captivity, a marsh mongoose has lived for 17 years and 5 months (Nowak and Paradiso, 1983).

ECOLOGY. Although marsh mongooses require dense vegetation cover and a permanent or semi-permanent source of water (Lynch, 1983; Rautenbach, 1982; Shortridge, 1934; Smithers, 1983), they may wander away from water to search for food (Rosevear, 1974; Rowe-Rowe, 1978; Smithers, 1983). In some parts of Africa they range from sea level up to about 2,500 m (Kingdon, 1977) and have been recorded in the hills of Accra where standing water or swampy conditions are rare (Booth, 1959). The marsh mongoose is thought to be an important member of the community of animals that are particularly adapted to living in *Papyrus* swamps.

While little or nothing definite is known of their nesting habits (Rosevear, 1974), a resting place was found close to water within MAMMALIAN SPECIES 408

a *Phragmites* reed bed, where an animal was lying under a dense matted mass of leaves and stems on dry ground. Another resting place was situated by a dam wall close to an outlet pipe (Smithers, 1983). Distinct runs are made from resting places to feeding grounds (Smithers and Wilson, 1979).

The diet consists mainly of crabs (Potamonautes sp.) and rodents (Otomys angoniensis, Mus minutoides and Mastomys sp.). Amphibians, insects (Coleoptera and Isoptera), birds, fish, and some fruits (Diospiros mespiliformis), as well as eggs of birds may be taken (Baker, 1989; Louw and Nel, 1986; MacDonald and Nel, 1986; Rowe-Rowe, 1978; Smithers, 1971, 1983; Whitfield and Blaber, 1980). Marsh mongooses are territorial and extend their foraging period rather than their foraging range when food is scarce (Kingdon, 1977).

Parasites occurring on Atilax include fleas (Ctenocephalides felis and Echidnophaga gallinacea), ticks (unidentified species, De Meillon et al., 1961; Rhipicephalus simus, Loveridge, 1923), and lice (Trichodectes acutirostris, T. mungos, T. rammei, Loveridge, 1923). Filarid worms were found beneath the skin (Loveridge, 1923) and three species of nematodes (one identified as Oxynema sp., Stuart, 1981) have been isolated from the alimentary tract (Baker, 1988b). An ascarid (Cloeoascaris spinicollis gen. et sp. n.) was found in the stomach (Loveridge, 1923).

Little is known about the diseases of Atilax, apart from bone diseases: damage to the hind foot is common and one Atilax specimen exhibited a swollen distal half of metatarsal II, attributable to a bone disease (Taylor, 1971).

Marsh mongooses are crepuscular or nocturnal (Rosevear, 1974; Smithers, 1983) and appear to coexist sympatrically with other carnivores (MacDonald and Nel, 1986). In certain parts of the range, otters (Lutra maculicollis and Aonyx capensis) have similar habitat and food requirements. However, no evidence of conflict between these species has been found (Louw and Nel, 1986; Rautenbach and Nel, 1978). Marsh mongooses avoid contact with other animals and their varied diet allows coexistence (Baker, 1989). Two animals together have been sighted during the breeding season (Smithers, 1983; Stuart, 1981), but most observations indicate marsh mongooses are solitary (Rosevear, 1974; Rowe-Rowe, 1978).

Marsh mongooses are not rare viverrids, but, because of their nocturnal, secretive habits, they are seldom seen (Rosevear, 1974). They are known to be responsible for occasional losses of poultry (Rowe-Rowe, 1978; Stuart, 1981).

Atilax breeds in captivity if it is housed in a quiet, undisturbed locality (Baker and Meester, 1986). If upset, the mother will usually eat the young. If housed together with other adult marsh mongooses the incidence of killing and eating of young increases (Frese, 1981). The young respond well to hand-rearing and are able to be handled during the 1st year (Baker, 1988a).

Capture is difficult because marsh mongooses are wary of traps. Once caught in a live trap, however, mongooses become frenzied when approached and frequently damage their muzzles (FitzSimons, 1919). When introduced to an enclosure, several months may elapse before the animals settle and become cage-adapted (Baker, 1988b). Marsh mongooses have been fitted with radio collars without apparent adverse behavioral effect (Maddock, 1988).

BEHAVIOR. Because Atilax is usually solitary, the majority of intraspecific interactions are restricted to the breeding season and take place within the context of mating. In captivity, males dominate females and persistently pursue them until the female is ready to allow mounting. During the mounting phase, the roles are switched and the female becomes aggressive while the male becomes submissive. More than one mounting occurs with a maximum of 30 mounts in one sequence being recorded. Intromission is achieved several times. In captivity, the height of mating frenzy lasts for approximately 9 days and thereafter the animals assume a more amicable relationship. Mated animals may be maintained together until the time of birth of the young when removal of the male prevents infanticide. Interactions apart from mating include allogrooming and agonistic encounters (Baker, 1988b; Baker and Meester, 1986).

During agonistic encounters, two adults seldom attack each other, but instead rely on a variety of threat postures and submissive responses (Baker, 1988c). Allogrooming is concentrated in the head and neck regions and often is elicited by nuzzling the throat region of the partner. Autogrooming is unsystematic, but may be extensive, particularly after foraging when the fur is damp (Baker, 1989). The

tongue is rough and equipped with short spinous processes which aid in cleaning the dense fur (Baker, 1988a; Sonntag, 1923).

While still dependent on the mother the young exhibit a wide variety of intraspecific interactions including play, allogrooming, and agonism. These behaviors also include the mother and in many instances she elicits play and allogrooming. Play takes on a variety of forms and can be broken into two main categories: behavior patterns associated with feeding and prey capture and patterns associated with reproduction and agonism (Baker, 1988b). Activity is from dawn until 0830 or 0900 h in cool overcast weather and from 1700 or 1730 to 1900 h in the evening (Smithers, 1983).

Communication includes vocalizations, behavioral displays, and chemical communication (Baker, 1988a, 1988c). Five different sounds are made, three of which are agonistic and two amicable. Behavioral displays are accentuated by mouth movements, which are particularly noticeable by virtue of the pink lips. Most displays are agonistic, apart from those related to allogrooming. Chemical communication involves the deposition of secretions from the anal and cheek glands, as well as urination and defecation. A hand-stand position is used for depositing anal scent in a mongoose in East Africa (Ewer, 1973; Hediger, 1949), which Fiedler (1957) attributes to Atilax. Commonly used methods of scent deposition are the anal drag and cheek rubbing. Scats are deposited in latrines (Baker, 1988a; Maddock, 1988).

Marsh mongooses spend a long time in or near water in search of food. Swimming in deep water is not common (Smithers, 1983) and the animals spend most of their time foraging in the shallows and adjacent reed beds (Rowe-Rowe, 1978). On occasion, when they do take to deeper water, marsh mongooses swim well, with the webless feet paddling beneath the body. The tail acts as a rudder and the dense fur becomes completely wet. An immersion time of 15 s has been recorded during foraging. On land locomotion usually involves a slow trot, although marsh mongooses are capable of rapid movement (Rosevear, 1974; Taylor, 1970).

Aquatic food is located by means of feeling with the forefeet below the water level or under small rocks and in crevices (Baker, 1989; Lombard, 1958; Rowe-Rowe, 1978). The head remains lifted until prey are detected, whereupon the mongoose lunges forward to grab the food with the jaws. Crabs often are eaten entirely, although the carapace may be discarded (Baker, 1989; Smithers, 1983). Frogs are usually immobilized by a bite on the cranium and then rolled on the ground with the forefeet. This procedure eliminates some of the noxious exudate produced by many amphibians. When Bufo regularis congregate to mate during the summer rains in southern Africa, marsh mongooses avoid eating the body of this species and simply devour the heads or kill and leave the prey intact. Rodents are located by sight and sound and are chased and killed by means of a bite on the cranium. No part of the prey is discarded, although on occasion the skull may be left if the prey is large (Baker, 1989). Eggs of large birds are broken by lifting them between the forefeet, thus resulting in a bipedal stance, and then throwing them to the ground (Baker, 1989; Dücker, 1965; Ewer, 1973; Steinbacher, 1939). Small eggs are crushed in the jaws and often eaten completely (Baker, 1989).

The most commonly adopted position for sleeping is a tight coil with the nose buried in the tail fur. Little attempt at nestbuilding has been observed although Kingdon (1977) reports attempts to construct shallow burrows.

GENETICS. Karyological studies (Fredga, 1972; Pathak and Stock, 1976; Wurster and Benirschke, 1968) have shown that chromosome number varies with sex. The diploid number is 35 for males and 36 for females; the fundamental number is 66. Fourteen pairs of autosomes are metacentric or submetacentric and three pairs are acrocentric or subacrocentric. The X chromosome is a medium metacentric. The male may by XO, may carry the Y translocated onto one of the autosomes, or may have some other sex chromosome arrangement. The sixth largest pair in the male is generally heteromorphic, suggesting a translocated Y (Wurster and Benirschke, 1968).

REMARKS. Mustela voang-shire and Mustela galera have been incorrectly placed in the synonymy of Atilax paludinosus (Allen, 1939) and are not included in the synonymy section. A. p. naso, A. p. nigerianus (Allen, 1939), and A. p. guineensis (Wenzel and Haltenorth, 1972) are also listed as subspecies. A. p. rubellus and A. p. transvaalensis are regarded as synonyms of A. p. paludinosus (Meester et al., 1986).

Atilax is derived from the Greek thylax, meaning pouch and a denoting without. This name resulted from the mistaken assessment that marsh mongooses lacked the anal pouch. The historical identity of Atilax is uncertain and Allen (1924) clarified the issue (Rosevear, 1974). The marsh mongoose is also known as the water mongoose.

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